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OYSTERCATCHER *HAEMATOPUS OSTRALEGUS* WINTER MORTALITY IN THE NETHERLANDS: THE EFFECT OF SEVERE WEATHER AND FOOD SUPPLY

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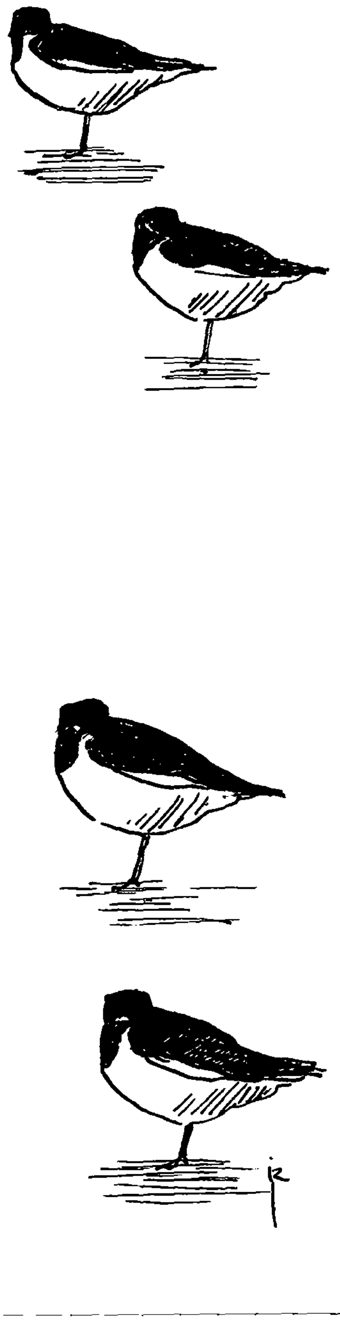

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Wintering Oystercatchers in The Netherlands are concentrated in the Wadden Sea (c. 200 000), with substantial numbers in the Delta area (c. 90 000). Only 1% of the total wintering population is normally found along the North Sea coast. Cold-rushes under severe winter conditions lead to a reduction of wintering numbers in the Wadden Sea, and to increases in the Delta and along the North Sea coast. The mortality of wintering Oystercatchers in The Netherlands was studied on the basis of beached bird surveys along the coast of the North Sea and the Wadden Sea between 1969 and 1996. On the whole, the pattern corresponded well to annual mortality estimates from population studies on the Wadden Sea islands of Schiermonnikoog and Texel. Peak numbers of dead Oystercatchers were found in most severe winters, but also in some moderate winters such as in 1976 and 1991. In mild winters, rather small numbers of dead Oystercatchers were recorded. For 1986-1996, annual mortality along the coast ranged from a c. 500 in the mild winters of 1989 to c. 10 000 individuals in 1987 and 1996. Multiple regression analysis of the number of dead Oystercatchers in winter 1975-1996 on the number of cold days and the biomass of benthic prey revealed an explained variance of 66% (n = 21). Both the number of cold days and prey biomass had a significant effect. The results explained the relatively high mortality among Oystercatchers in the moderate winters of 1976 and 1991 (very low food stock), and the low mortality in the severe winter of 1982 (large food stock). The extremely high mortality in 1987 was due to a combination of low food stock and severe weather. The depletion of Cockles and Mussels in the Wadden Sea in the early 1990s, due to a combination of overfishing and failing reproduction, triggered a southward mass movement of Oystercatchers and substantial mortality in the Delta area in the winter of 1990-1991. The absence of a peak in the mortality among adult breeders in the population studies for that particular winter is the major discrepancy between these population studies and the beached bird surveys. It is an indication that primarily non-local, and therefore probably less dominant, Oystercatchers suffered from the food shortage in the Wadden Sea. The results suggest that for Oystercatchers the scarcity of their principal prey due to overfishing has taken its toll. Had this season also been a cold winter, the results suggest that the mortality would have been unprecedented.

Key words: Oystercatcher - *Haematopus ostralegus* - winter mortality - starvation - cold rushes - food supply - beached bird surveys - ringing recoveries

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INTRODUCTION

The belief that starvation is the primary risk that Oystercatchers *Haematopus ostralegus* face during winter is the common thread that runs through many contributions of the recent account of Oystercatcher ecology edited by Goss-Custard (1996). It leads to the assumption that the birds will often seek to maximize the rate of energy gain whilst feeding. It also leads to the assumption that competition will be mainly for food and that the negative effects of competition can be gauged in terms of by how much the rate of food intake is decreased by an increase in the density of competitors. Finally, it comes as no surprise that, in this view, Oystercatcher numbers in winter are thought, at least in part, to be limited by their food supply. It follows that a decline in the food supply, for whatever reason, should lead to increased mortality and a decline in numbers.

Widely held beliefs are not necessarily true, but there is certainly strong evidence that Oystercatchers often die of starvation. During severe winters, much of the food supply becomes covered with ice, while energy demands of the birds are very high. Several severe winters during the last decades are known to have led to mass mortality among Oystercatchers and other waders (Dacker 1948, Davidson 1982, Davidson & Evans 1982, Berrevoets 1987, Van Gompel 1987, Camphuysen 1989, Hulscher 1989, Meininger *et al.* 1991, Goss-Custard *et al.* 1996). The extremely low weights of the dead birds strongly suggest starvation (Swennen & Duiven 1983, Hulscher 1989). It does not necessarily follow, however, that the size of the food supply would have made a difference for their survival: the birds simply cannot feed when their food is covered by ice. To survive such difficult periods, the birds accumulate fat reserves in advance (Hulscher 1989, Zwarts *et al.* 1996b). It may be hypothesized that poor food supplies prevent the birds from accumulating sufficient reserves, making them especially vulnerable to severe winter weather. Remarkably, there is as yet no good evidence that this scenario works and that, all else being equal, poor food supplies increase mortality. This paper aims to provide such evidence.

Wintering Oystercatchers in the Wadden Sea and the Delta area in The Netherlands feed mainly on Cockles *Cerastoderma edule* and Mussels *Mytilus edulis* (Hulscher 1996, Zwarts *et al.* 1996a & c). Together with Eider Ducks *Somateria mollissima*, Oystercatchers are the most important bivalve consumers in terms of biomass of benthic food in these areas (Hulscher 1981, Smit 1981). Minimal biomass values on the tidal flats occur in late winter and several species live relatively deep in the sediment in winter, just when food demands of individual birds are high (Beukema 1974 & 1993, Kersten & Piersma 1987, Esselink & Zwarts 1989, Zwarts & Wanink 1993). Therefore, the amount of food available to Oystercatchers in late winter seems critical (Beukema 1993, Goss-Custard *et al.* 1996).

Cockles are sensitive to severe winter conditions, after which they die out almost completely on the tidal flats (Hancock & Urquhart 1964, Beukema 1993). Mussels are more resistant to severe winters and those mussel beds that occur at sheltered locations on the tidal flats are very stable, occurring in the same areas since time immemorial (Dankers & Koelemaij 1989, Obert & Michaelis 1991, Beukema 1993). However, numbers and biomass of both species are notoriously unstable in the Wadden Sea as a result of highly variable recruitment in combination with a relatively short life span (Beukema *et al.* 1993). Furthermore, strong density dependent mortality in younger year classes that might stabilize the numbers in the older year classes suitable for Oystercatchers (e.g. McGrorty *et al.* 1990) seems to be lacking in both species in the Wadden Sea. When recruitment fails for a series of years, stocks of Cockles and Mussels may fall to very low levels, especially when commercial shellfishing continues. This happened in the winter 1990/1991. According to Beukema (1993), Oystercatchers may have experienced a food shortage and switched to alternative, less profitable prey in that winter. He showed that the most important alternative prey for Oystercatchers, *Macoma balthica* and *Mya* *arenaria*, experienced unusually high mortality rates in the appropriate size classes, probably as a result of Oystercatcher predation. The observed stock depletion of Cockles and Mussels in 1991 caused a mortality rate in wintering Eiders that was three times higher than in 'normal' years (Camphuysen 1995, 1996). However, although it was reported that Oystercatchers died in 'unusually high' numbers in 1991 and occurred in greater than normal numbers at inland feeding sites (Beukema 1993), the possible adverse effects of food scarcity for these birds were not properly studied. In fact, no excessive mortality of Oystercatchers was observed among the marked individuals known to winter in the Wadden Sea and breeding on Schiermonnikoog (see later). There is a need to show how these conflicting observations can be reconciled.

The crucial point is that poor feeding conditions as a result of ice covering the feeding areas or low food stocks need not necessarily cause the birds to starve to death when their energy reserves become insufficient. There is the alternative option for the bird of leaving the area in search of better feeding conditions elsewhere (Elkins 1983, Camphuysen & Derks 1989, Hulscher 1989, Hulscher *et al.* 1993). But since these areas were not the first choice of the birds, we may still expect mortality to be higher, unless, of course, the winter habitat choice is also considerably influenced by such non-winter-survival considerations as being close to the breeding areas. In the same way, Eider Ducks also showed an aberrant spatial distribution pattern as well as an increased mortality (Swennen 1991, Camphuysen 1996).

This paper tests the hypothesis that a negative relationship does indeed exist between food supply and mortality rates in wintering Oystercatchers, but that the impact may depend on the severity of the winter. To this end, we describe temporal and spatial patterns in mortality among wintering Oystercatchers in The Netherlands in the 1970s, 1980s and early 1990s. Long-term data sets on environmental conditions (i.e. severity of winters) and fluctuations in food supply (i.e. bivalve stocks) are combined and compared with wintering numbers, the occurrence of cold-rushes and mortality patterns of Oystercatchers along the coast. Excessive mortality and/or mass departures from the Wadden Sea area were expected in cold winters, when the availability of prey was reduced, or when food stocks were particularly low.

MATERIAL, METHODS AND STUDY AREA

The data provided information on: (1) fluctuations in Oystercatcher mortality over a series of years, (2) wintering numbers of Oystercatchers in the main staging areas, (3) the occurrence of mass movements away from the Wadden Sea (or into the Dutch sector from Danish/German wintering sites) in response to adverse weather weather conditions ('cold-rushes'), (4) the occurrence of cold weather and icing, and (5) fluctuations in the standing stock of suitable bivalve prey in the Wadden Sea.

Winter conditions

The severity of the respective winter seasons was judged on the basis of daily mean air temperatures measured at De Bilt, The Netherlands (Koninklijk Nederlands Meteorologisch Instituut (KNMI), monthly reports 1975-1996). Winters were qualified on the basis of the frequency of 'cold days' (days with a mean temperature below 0°C) at De Bilt, between 1 December-31 March. In this analysis, days with mean temperatures below -10°C counted for three days, days with mean temperatures between -5 and -10°C counted for two days and days with mean temperatures between -5 and -0°C counted for one day. 'Cold periods' were single days or series of days on which the mean temperature was below 0°C. Between January 1975 and March 1996, 120 such 'cold periods' were identified, 59 of which lasted only one day. The longest cold period was recorded in 1986 (30 days, 3 February-4 March, overall mean temperature -3.7°C, minumum daily mean -8.8°C). Arbitrarily, winters with less than 20 'cold days' were classified as 'mild', winters with

20-40 cold days as 'moderate' and winters with > 40 cold days as 'severe'.

Wintering Oystercatchers

Estimates of the wintering population of Oystercatchers were derived from January counts in the Wadden Sea area, in the Delta, and along the North Sea coast (Meininger 1977, Meininger & Becuwe 1979, Meininger *et al.* 1984, 1985, 1994 & 1995, Keijl 1987, Meltofte *et al.* 1994, IWRB unpubl. data). Wadden Sea data include January counts between 1974-1993, the information for the Delta area spans 1974-1994, whereas only three censuses for the North Sea coast were available (1977, 1978, and 1986).

Cold-rushes

The occurrence and timing of so-called 'cold-rushes' was analysed on the basis of sea-watches from scattered sites along the Dutch coast between 1972 and 1996 (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994, quarterly reviews in *Sula* 1988-1996, seawatching reports 'Club van Zeetrekwaarnemers' 1-38, and NZG/CvZ unpubl. data). Several coastal sites along the Dutch coast are manned throughout the year and the most important site for this analysis, Camperduin (Noord-Holland), has been manned virtually daily since the mid-1970s. A 'cold-rush' was defined as a sudden mass movement of waders and wildfowl, whether or not they coincided with the onset of severe winter conditions or certain spells of cold weather (see Camphuysen & Van Dijk 1983). In a cold-rush of Oystercatchers, a few hundreds up to many tens of thousands of birds could be involved. Because sea-watching sites are not usually manned throughout the entire day (mostly a few hours in the morning only), estimates of the total numbers of birds engaged in a single cold-rush could rarely be made. Moreover, small-scale cold-rushes could have been missed entirely.

Mortality

Patterns of Oystercatcher mortality were derived from beached bird surveys (BBS) conducted between 1969 and 1996 along the Dutch North Sea and Wadden Sea coasts (Fig. 1; Camphuysen 1989, 1992 & 1995, NZG/NSO unpubl. data). BBS were analysed by subregion in order to study spatial differences in mortality rates. Subregion I is the North Sea coast of the Delta (116 km total length), but excluding the estuarine areas behind the barriers; subregions II-III include the mainland coast of Zuid-Holland (ZH; 60 km) and Noord-Holland (NH; 62 km) respectively; subregions IV (94 km) and V (148 km) include all Wadden Sea islands; subregion VI is the Wadden Sea coast between Den Helder and the Dollard estuary, including the seaward side of the

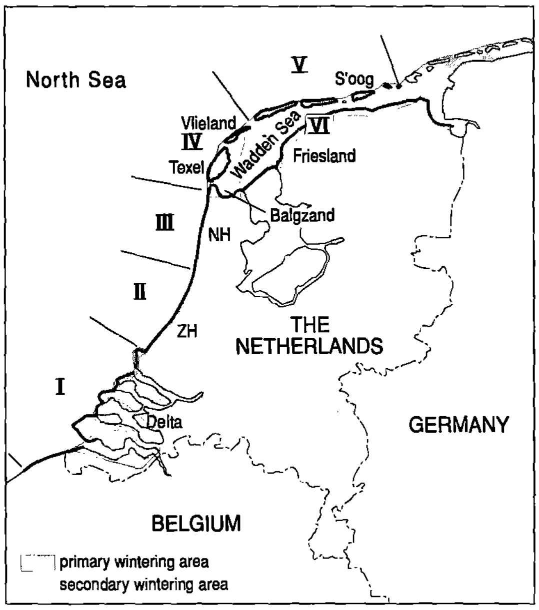

Fig. 1. Study area and place names mentioned in this article. Shown are the North Sea coast and the Wadden Sea coast searched during beached bird surveys (thick coastline), subregions I-VI used for the analysis of these surveys, ringing sites of Oystercatchers at Texel, Frisian coast (Friesland) and Schiermonnikoog (S'oog) and a generalized image of the wintering range of Oystercatchers in January (after SOVON 1987). Darker shading indicates areas where Oystercatchers were most abundant, white areas indicate regions where Oystercatchers were scarce or absent. The map does not provide information for Belgian coastal areas.

Afsluitdijk (192 km). The study area has a total length of approximately 670 km, including 368 km of sandy beach (I-V), and 302 km of dikes (I, III, IV, and VI), sometimes buffered by salt marshes on the seaward side (IV-VI).

Monthly BBS, which are sample counts conducted between January 1986 and March 1996, were used to estimate by means of extrapolation the total number of dead Oystercatchers along the coast in each subregion. The monthly BBS contained approximately 35% missing values. Missing values occurred particularly frequently in the summer months (May-October; 59% missing values), whereas the winter (November-April) was well covered (14% missing values). Four log-linear Poisson models which assumed independence of the data were applied to impute missing counts, as in Van der Meer *et al.* (1996). In each model, the expected value of beached birds was assumed to depend on a function of year, month and subregion. The models differed in the extent to which they included interactions between these factors (see results). Model parameters were estimated with the regression procedure of the Genstat 5.1 programme (Payne *et al.* 1987). Estimates of the monthly total number of dead Oystercatchers in each of the subregions were obtained by extrapolation of observed or modelled (where observations are missing) densities.

Longer time series are available for the national beached bird surveys (NBBS) that have been conducted around the last weekend of February (± 1 week) since 1965. During national surveys, attempts were made to survey the greatest possible proportion of each of the six subregions. Results of national surveys were compared with mid-winter indices of monthly beached bird surveys during 1986-1996 in order to judge the value of the NBBS to evaluate the scale of winter mortality among Oystercatchers. Potentially, the NBBS provided data on the occurrence of elevated mortality rates of Oystercatchers in The Netherlands over a series of 31 winters since 1965 (no survey took place in 1974). However, the first surveys were biased towards oiled specimens and it is unclear to what extent unoiled carcasses were ignored (Camphuysen 1989). Therefore, for a detailed analysis, only numbers of dead Oystercatchers from the NBBS between 1975 and 1996 (21 years) in each of the six subregions were used.

The fact that BBS are conducted on beaches, dikes and salt marshes rather than on high tide assemblies of Oystercatchers limits the usefulness of the estimates of total number of birds dying each year. Increased numbers of dead Oystercatchers along the coast may result either from increased numbers of birds wintering there or from elevated mortality rates, or from both. For this reason we compared the mortality figures for Oystercatchers derived from BBS with mortality rates from ringing recoveries and resightings of marked birds from two population studies in the Wadden Sea described below. BBS results are particularly interesting because of the systematic approach that was adopted over a long series of years, irrespective of any trends in Oystercatcher mortality. Hence, without pretending to have monitored actual mortality rates of Oystercatchers (i.e. percentage of dead Oystercatchers from the total population), the results demonstrate fluctuations and extremes in (winter) mortality.

Population studies

Oystercatchers have been caught and colour-marked on the islands of Texel and Schiermonnikoog since 1983. The study on Schiermonnikoog is described by Ens *et al.* (1992, 1995). Each year, the main study area was scanned for marked birds that bred there the year before. If a marked bird did neither return nor breed in a surrounding area nor turn up on the club (roost of adult birds without a breeding territory), it was classified as missing and assumed dead. On a total of 168 birds reported missing on the main study area, no less than 40 were actually reported dead (23.8%). This rather high reporting rate for a bird of that size (cf. Vermeulen *et al.* 1990) may be related to the fact that birds with colour rings are more likely to be recovered and reported (Shedden *et al.* 1985). So far, we have no cases of breeding birds that moved away from the study area and the high re-

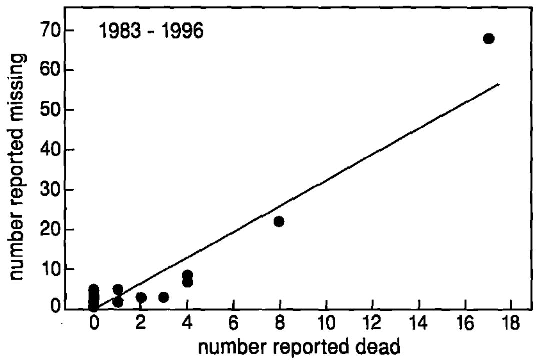

Fig. 2. The number of Oystercatchers breeding in the main study area on Schiermonnikoog in year t and reported missing (but not known to be dead) in year t+1 as a function of the number actually reported dead in year t+1. For each year, the numbers refer to the accumulated total for the 'summer' period (from March-August) and the subsequent 'winter' period (from September- February). The line depicts a reporting rate of 24% (i.e. to every breeder reported dead an additional 3.2 birds are missing) calculated from the accumulated totals.

porting rate certainly suggests that the number of such birds must have been small. Furthermore, for years where the number of birds that were missing but not reported dead was high, the number of birds actually reported dead was also high (Fig. 2). On the basis of this reporting rate of 24% we could estimate how many birds had died. Subtracting the dead birds from the cumulative number that were marked yielded the number still alive. In combination with the number that subsequently died, we could estimate the mortality rate for each year. Since juveniles suffer a very high mortality in their first winter (Kersten & Brenninkmeijer 1995), we excluded birds that were marked as juvenile from the analysis. However, we included parts of the study area that were not included in the calculation of the reporting area.

Procedures are very similar for the study on Texel. However, the intensity of scanning for marked birds differed considerably between years and this greatly affected the probability that a bird would be reported missing for a given year. For this reason we only used the second mortality estimate for the Texel data, which we based on the reporting rate that we obtained for Schiermonnikoog. Clearly, the assumption of a fixed reporting rate ignores variability in the course of the season, between years and between areas in the probability of being recovered.

Food supply

Information on fluctuations in the standing stock of benthic invertebrates in late winter, most notably the principal prey items of Oystercatchers, *Mytilus edulis* and *Cerastoderma edule*, was taken from abundance estimates of benthic invertebrates in February-March 1970-1995 at Balgzand in the western Wadden Sea (Fig. 1; Beukema 1993, NIOZ unpubl. data). An earlier analysis of the abundance of benthic prey items in the Wadden Sea as a whole, showed that biomass densities in the Balgzand area are reasonably well correlated with the abundance elsewhere in the Wadden Sea (Beukema *et al.* 1993). Fixed sampling stations were scattered over the tidal flats, covering all types of sediment and all intertidal levels. Samples were taken by sieving cores: 50 along each of twelve transects and 18 within each of three squares of 900 m^2. The abundance of benthic animals is expressed in biomass units: g m^{-2} ash free dry weight of the soft parts (Beukema 1993). For the analysis in this paper, sampling data for February-March 1975-1995 were used, including all the common prey items of Oystercatcher in the Wadden Sea, i.e. *Cerastoderma edule* and *Mytilus edulis*, together with secondary prey including *Arenicola marina*, *Carcinus maenas*, *Macoma balthica*, *Mya arenaria*, *Nereis diversicolor*, and *Scrobicularia plana*, but with emphasis on Cockles and Mussels.

RESULTS

Wintering Oystercatchers

The principal wintering areas of Oystercatchers in The Netherlands are the Wadden Sea area, the Delta area and the coastal strip, with only low

Table 1. Mean numbers of wintering Oystercatchers in the Wadden Sea, along the North Sea coast and in the Delta area, based on mid-January counts between 1974 and 1994. Between 1980 and 1991, individual counts in the Wadden Sea area were 'corrected' by adding an estimated number of Oystercatchers for areas which were not censused on the basis of previous and later counts (see Fig. 3).

	Wadden Sea area		North Sea coast	Delta area
	totals	corrected	totals	totals
$\bar{x}$	173752	220283	3190	92805
SD	51515	50272	158	14057
min	74600	141100	3075	66500
max	312100	324600	3370	125300
n	21	12	3	19

numbers occurring inland (SOVON 1978; Fig. 1). In the Wadden Sea, c. 200 000 Oystercatchers spend the winter on average (Table 1; Meltofte *et al.* 1994). Totals in January 1974-1994 varied between 74 600 (1987) and 312 100 (1984), without obvious trends. For 1980-1991, incomplete censuses were corrected by an 'estimated' total number of Oystercatchers, using the mean for January in earlier and/or later years for sites that were not visited in a given year. Meltofte *et al.* (1994) corrected a very low value of 75 000 Oystercatchers on 17 January 1987 for missing values to 140 000 on the basis of the mean for January in other severe winters. However, a cold-rush of Oystercatchers on 14 January 1987, during which at least 64 000 birds were seen heading south along the mainland coast of Zuid-Holland (Keijl & Mostert 1988), might equally have been the explanation for the very low numbers observed. A negative relationship was found between the frequency of 'cold days' and the number of Oystercatchers recorded in the Wadden Sea ($r = -0.59$, $n = 21$; Fig. 3). These data suggest that fewer Oystercatchers winter in the Wadden Sea in cold winters.

Around 93 000 Oystercatchers overwinter annually in the Delta area (Meininger *et al.* 1984, 1985, 1994 & 1995). Between 1976-1991, January totals fluctuated between 66 500 (1993) and 125 300 individuals (1979; Table 1). In recent years, there has been a general decline in numbers wintering in the Delta area, which is mainly the result of a decline in numbers in the Oosterschelde area (Meininger *et al.* 1995). A positive relationship was found between the number of 'cold days' and total numbers of Oystercatchers in January ($r = 0.59$, $n = 19$; Fig. 3). The fact that wintering numbers in the Wadden Sea area are relatively low in cold winters suggests that under these conditions the Delta area is used as a refuge for birds that normally winter further to the north. According to the regression lines, no less than 100 000 Oystercatchers may leave the Wadden Sea, but at maximum 30 000 extra birds turn up in the Delta area. This suggests that the rest may have moved further south or to the North Sea coast.

The numbers of (wintering) Oystercatchers along the Dutch North Sea coast are not very well known. Oystercatchers are widespread but overall numbers are apparently rather low (SOVON 1988). The frequent sightings of this species during seawatching (movements recorded in 60% of all observations hours through the year along the mainland coast; Camphuysen & Van Dijk 1983) are mainly due to local movements of feeding birds along the coast. However, it is impossible to estimate total numbers present along the shore from sea-watching results alone. In the mild winters of 1977, 1978 (Meininger 1977, Meininger &

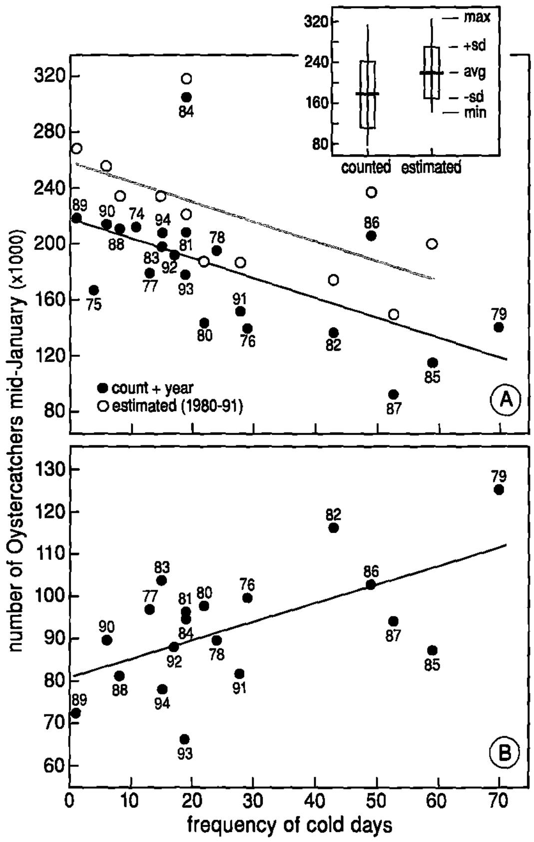

Fig. 3. Numbers of Oystercatchers in (A) the Dutch Wadden Sea and in (B) the Delta area in relation to the frequency of cold days. Individual counts are plotted as figures indicating the year of count. Wadden Sea data refer to January counts during 1974-1993 (after Meltofte *et al.* 1994, and IWRB/C.J. Smit unpubl. data). For 1980-1991, incomplete censuses were corrected by an 'estimated' total number of Oystercatchers, using the mean for January in earlier and/or later years. These estimates, with an higher mean, lower *SD* and smaller range than the actual counts (inset), follow the same pattern as the actual count and the negative relationship with the frequency of cold days (dotted line) is similar. Numbers of Oystercatchers in the Delta area refer to January counts during 1974-1994 (after Meininger *et al.* 1984, 1985, 1994 & 1995).

Becuwe 1979) and just prior to a significant spell of cold weather in 1986 (Keijl 1987), numbers of wintering Oystercatchers present along the North Sea coasts were counted. The survey on 8-9 January 1977 counted 3126 Oystercatchers (Wadden Sea islands 5.5 km^{-1}, mainland coast Noord- and Zuid-Holland 3.1 km^{-1}, Delta area 15.6 km^{-1}). On 13-14 January 1978, a very similar 3075 Oystercatchers were counted, but more evenly distributed than in 1977 (Wadden Sea islands 9.7 km^{-1}, mainland coast Noord- and Zuid-Holland 5.3 km^{-1}, Delta area 9.4 km^{-1}). The fairly incomplete survey on 11-12 January 1986 resulted in 3370 Oystercatchers (6.6, 2.4, and 17.9 km^{-1} for the Wadden Sea islands, the mainland coast and the Delta area respectively). No censuses were performed during severe winter conditions, but anecdotical information indicates that wintering numbers along the shore may increase substantially in cold weather.

In conclusion, the population of wintering Oystercatchers in The Netherlands is concentrated in the Wadden Sea area (c. 200 000), with substantial numbers in the Delta area (c. 90 000). Only a small fraction (c. 1%) of the total wintering population is normally found along the North Sea coast. Severe winter conditions lead to a reduction of wintering numbers in the Wadden Sea area, and to increases in the Delta and along the North Sea coast.

Cold-rushes

Concentrated movements of at least several hundreds of Oystercatchers over a few hours time heading south at a given site, during or following spells of cold weather, were selected as 'cold-rushes'. Such cold-rushes along the mainland coast of Noord- and Zuid-Holland (i.e. Oystercatchers leaving the Wadden Sea area for more southerly wintering haunts) were recorded frequently, particularly during prolonged periods of cold weather. Generally, the more southerly sites along the mainland coast (Bloemendaal, Scheveningen) recorded much higher numbers of birds in cold-rushes than were recorded at the more northerly sites (Camperduin, Huisduinen), indicating extensive flights over land (N.F. van der Ham pers. comm.). Because the passage of Oystercatchers seldom motivated the observers to stay and watch until all

Table 2. Timing of cold-rushes of Oystercatchers recorded by seawatchers at the Wadden Sea islands (WD) and along the mainland coast of Noord- (NH) and Zuid-Holland (ZH). Indications of the number of birds involved are given as 'hundreds' (250-750), 'thousands' (750-7500) or 'ten-thousands' (> 7500 at a site, during a few hours of observation; see text).

period	site	magnitude of movements	reference
30-31 January 1976	Scheveningen (ZH)	hundreds	Van Dijk 1977
	Noordwijk (ZH)	hundreds	Van Dijk 1977
30 December 1976	Schiermonnikoog (WD)	ten-thousands (40 000 →W, 8 hours)	Van Eerden 1977
31 December 1978	Scheveningen (ZH)	thousands	Van Dijk 1980
14 February 1979	Camperduin (NH)	thousands	Van Dijk 1980
16-17 December 1981	Scheveningen (ZH)	hundreds	Maas & den Ouden 1982
31 December 1981	Schiermonnikoog (WD)	thousands	Maas & den Ouden 1982
8 January 1982	Texel (WD)	hundreds	Den Ouden & Maas 1983
16 January 1982	Texel (WD)	hundreds	Den Ouden & Maas 1983
7 February 1982	Camperduin (NH)	thousands	Den Ouden & Maas 1983
14 February 1982	Camperduin (NH)	hundreds	Den Ouden & Maas 1983
16-18 January 1985	Scheveningen (ZH)	thousands	Van der Ham *et al.* 1986
14 January 1987	Camperduin (NH)	thousands	Stegeman & Van Splunder 1989
14 January 1987	Scheveningen (ZH)	ten-thousands (63 000 →S, 6 hours)	Keijl & Mostert 1988
10 February 1991	Scheveningen (ZH)	thousands	*Sula* 5: 77
30-31 December 1995	Camperduin (NH)	thousands	*Sula* 10: 127
25-26 January 1996	Scheveningen (ZH)	ten-thousands (17 500 →S, 9 hours)	Van Elswijk unpubl. data
7-9 February 1996	Scheveningen (ZH)	ten-thousands (12 500 →S, 14 hours)	Van Elswijk unpubl. data

movements had ceased, only minimum estimates of total numbers involved are possible, tentatively ranked as 'hundreds' (250-750), 'thousands' (750-7500) and 'ten-thousands' (> 7500) (Table 2).

Between January 1975 and March 1996, 120 cold periods (single days or series of days with a mean temperature below 0°C) were recorded, with a mean duration of 3.9 ± 4.9 days (mean ± *SD*). Of these, 53 were single cold days. Two flights along the mainland coast labelled as 'cold-rush' in January and February 1982 did not coincide with cold weather. The remaining 19 days on which mainland coast cold-rushes were recorded all fell in periods of rather cold weather of at least eight days duration (mean length 14 days). However, cold-rushes were recorded in only 9 of 16 prolonged periods of cold weather (i.e. > 8 days or twice the mean length). Most remarkable was the lack of southbound mass movements of Oystercatchers during an unbroken period of 30 days of cold weather in the winter 1985/1986 (mean temperature -3.7°C, lowest daily mean recorded -8.8°C). Cold-rushes were usually recorded on days on which the temperature was well below the mean temperature for that particular cold period (17 out of 19 occasions). The timing varied considerably. Four days with mass movements fell right at the beginning of a prolonged cold weather period, seven flights occurred half-way through and eight at the end. The winters 1978/1979 and 1995/1996 were the coldest under study, both following a long series of mild or moderate winter seasons (1971-1978, 1988-1995). One of the most dramatic cold-rushes,

Table 3. Analysis of deviance of dead Oystercatchers found in monthly sample counts along the coast. The factors year (y), month (m) and subregion (r) have 11, 12, and 6 levels respectively. First order interactions are indicated by two letters (e.g. *ym*). For each model, the residual degrees of freedom (*df*) and the residual deviance are given. Each model is tested against (*versus*) a more complicated model, with one or more extra factors included. The test statistic is the difference in scaled deviance. The dispersion parameter is set equal to 1092/243. So, for example, the test of model 1 *versus* model 2 reveals a difference in scaled deviance of (6726-3280)/(1092/243) = 767. The scaled deviance approximately has a χ^2_t distribution, where t is the difference in degrees of freedom between the two models (e.g. when comparing model 1 and 2, 444 - 343 = 101). The difference in mean scaled deviance, that is the difference in scaled deviance divided by t, is given (e.g. 767/101 = 7.6). The results of the significance tests are shown in the last column, where *** means that $p < 0.001$.

model	factors	*df*	deviance	vs	mean scaled deviance	*p*
0	null	470	21795	1	129	***
1	y+m+r	444	6726	2	7.6	***
2	y+m+r+ym	343	3280	3	7.3	***
3	y+m+r+ym+yr	293	1647	4	2.5	***
	y+m+r+ym+mr	293	2535			
	y+m+r+yr+mr	344	3943			
4	y+m+r+ym+yr+mr	243	1092			

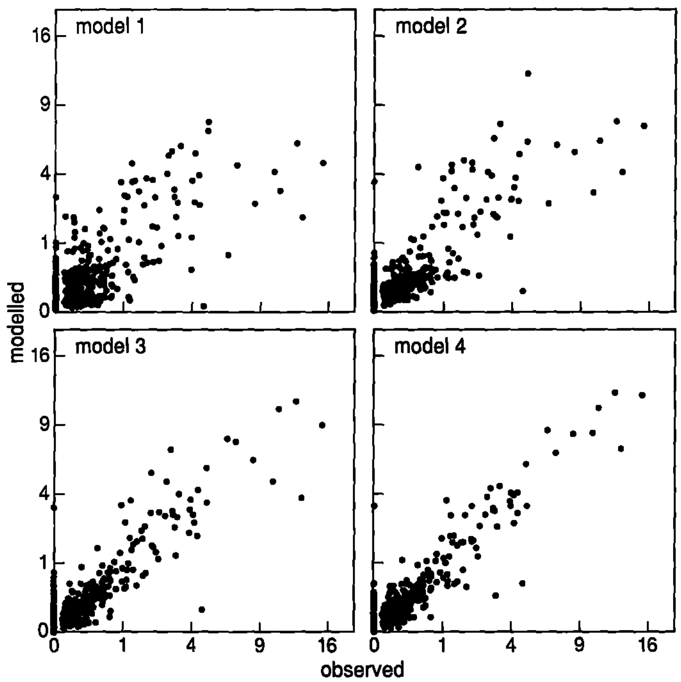

Fig. 4. Predictions of four log-linear Poisson models (1-4) in which an increasing number of interactions is included (modelled; see Table 3) and the actual monthly counts of dead Oystercatchers (observed) plotted against eachother. The figure shows that the similarity between model predictions and the actual data is high in the models 3 and 4.

however, was recorded on 14 January 1987 at Scheveningen (63 000 →S in six hours; Keijl & Mostert 1988). This cold-rush took place on the coldest day (mean temperature -13.2°C), right in the middle of a cold period of 15 days which had an overall mean temperature of -6.6°C.

Unfortunately, there is little information about Oystercatchers entering the North Sea from the Danish and German parts of the Wadden Sea when conditions were worse there. On 30 December 1976, when snow and ice covered much of the German and Danish Wadden Sea, some 40 000 Oystercatchers were observed in eight hours heading west and entering the Dutch sector, along the south side of Schiermonnikoog (Van Eerden 1977). The weather improved rapidly and no further movements along the mainland coast were observed. Similar influxes into the Wadden Sea were reported from Schiermonnikoog in December 1981 (Maas & Den Ouden 1982). Further movements along the mainland coast in January and February 1982 did not coincide with cold weather here and these may have involved mainly birds which were normally wintering in German and Danish waters. The Danish Wadden Sea was extensively ice covered in all parts and snow was reported on land (Meltofte *et al.* 1994). In the Delta area in January, rather high numbers of Oystercatchers were recorded (Fig. 3). In January 1986, relatively large numbers of Oystercatchers were counted in the Dutch sector. Extensive snow and ice cover was observed in the Danish and German part of the Wadden Sea whereas the Dutch sector was virtually clear of ice (Meltofte *et al.* 1994). Although it had not been observed, it is likely that Oystercatchers from Danish and German wintering sites had entered the Dutch sector.

In conclusion, cold-rushes of Oystercatchers along the mainland coast were recorded in 1976, 1979, 1985, 1987, 1991, 1996 and during prolonged spells of cold weather. The timing of these flight varied considerably, varying from the first day of a period of cold weather that lasted for at least nine days to the last day of a cold period. In addition, substantial southward movements were recorded in 1982 during mild weather, probably mainly of Oystercatchers originating from the Danish and German Wadden Sea where the winter was more severe. In 1986, no substantial southward movements of Oystercatchers were reported, despite a very long period of cold weather.

Oystercatcher mortality along the coast

Beached bird surveys usually deal with corpses of birds which have been washed ashore. However, most Oystercatchers which were found during these surveys died on the spot. In several severe winters, Oystercatcher corpses were typically found high up on the beach and near the dunes. Densities (n km^{-1}) of dead Oystercatchers found in each of the subregions were calculated on the basis of monthly sample counts over January 1986-March 1996. Four different models to impute missing values were compared (Fig. 4, Table 3). Model 4, in which the modelled values matched the observed numbers best, was chosen to impute missing values. However, for a few poorly covered summer months in subregions I, II and VI, model 4 could not estimate the accompanying parameters and in these cases the less complicated model 3 was used (Fig. 5). On the basis of similarities in changes in the relative abundance of dead Oystercatchers from year to year, subregions I, II-IV and V-VI are treated together in further analyses.

Monthly mean densities in each subregion were extrapolated to the total length of the coast to give monthly estimates of the total numbers of dead Oystercatchers found along the North Sea and Wadden Sea coast in each of the subregions (Table 4). Total numbers of dead Oystercatchers per year (between July in one year and June the next year) ranged from only 480 in 1988/1989 to 11 110 in 1986/1987. The occurrence of exceptionally large numbers of Oystercatchers differed considerably between subregions (Fig. 5). In the Delta area (subregion I), comparatively large numbers were recorded in 1990/1991 (c. 1810). In the eastern Wadden Sea islands (V) and along the mainland coast of Friesland and Groningen (VI), high numbers in 1992/1993 did not coincide with cold weather while the numbers of dead

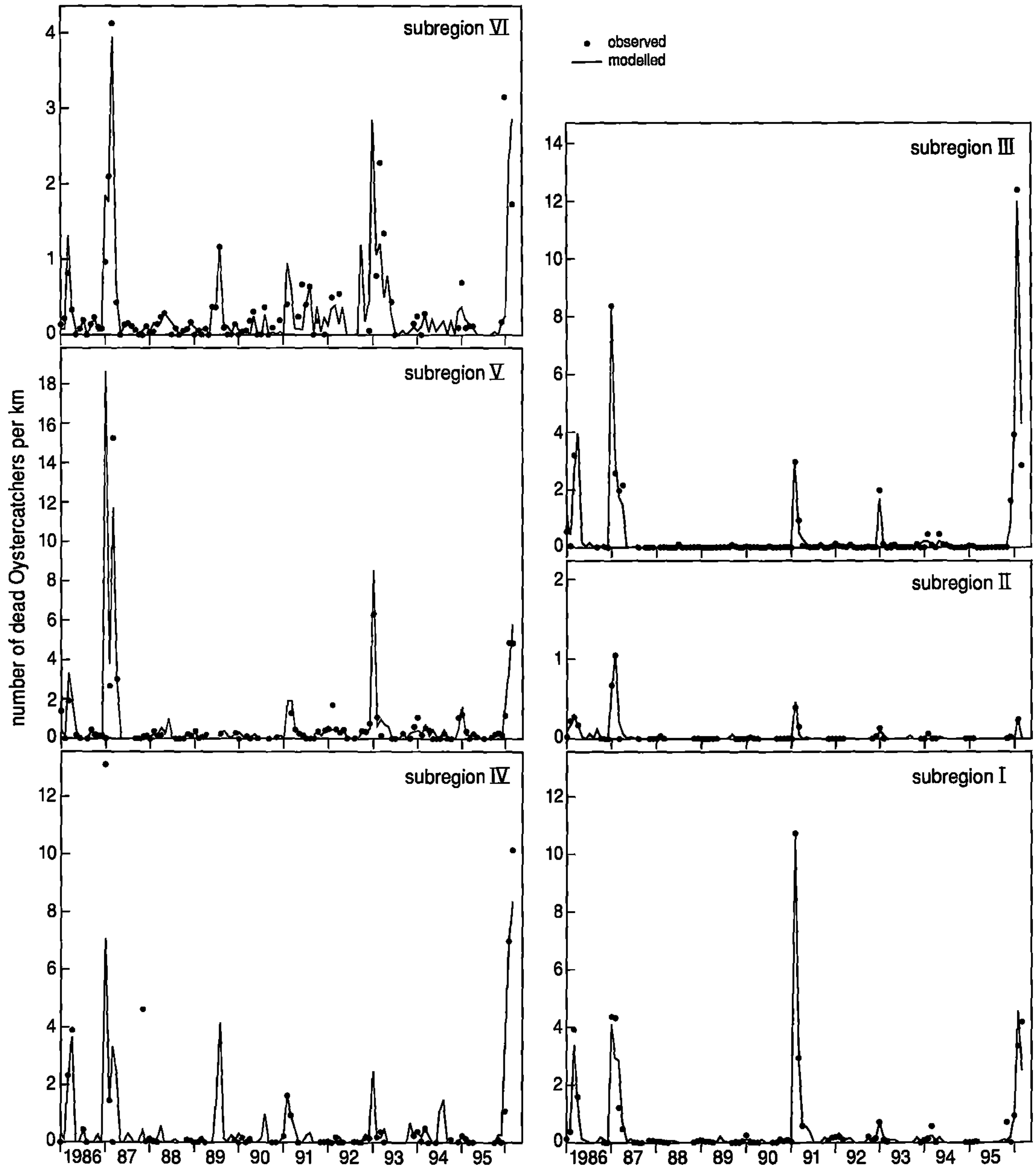

Fig. 5. Observed (•) and modelled (—) monthly densities of dead Oystercatchers along the North Sea coast of the Delta (I), Zuid-Holland (II) and Noord-Holland (III), Texel and Vlieland (IV), Terschelling-Schiermonnikoog (V) and the Wadden Sea coast of Noord-Holland, Friesland and Groningen (VI), January 1986-March 1996 (model 4 calculations, see text).

Table 4. Total numbers of dead Oystercatchers per subregion, based on monthly counts from January 1986 to March 1996, expressed as rounded totals from July to June the following year. Missing values were imputed using model four calculations.

July-June	I	II	III	IV	V	VI	Totals
/1986	740	50	480	600	820	300	2990
1986/1987	1260	120	930	1670	6060	1630	11670
1987/1988	40	0	0	560	350	260	1210
1988/1989	70	0	10	40	180	170	470
1989/1990	60	10	10	200	240	450	970
1990/1991	1810	40	250	340	680	520	3640
1991/1992	130	0	40	40	700	600	1510
1992/1993	160	10	140	330	1590	1890	4120
1993/1994	140	10	90	170	500	200	1110
1994/1995	10	0	20	50	500	300	880
1995/1996	1060	20	1260	1730	1770	4380	10220
min	10	0	0	40	180	170	470
max	1810	120	1260	1730	6060	4380	11670

Table 5. Annual mortality estimates for the population studies on Texel. The summer includes April-September in year 1, while the winter includes October-March in year1-2. It is assumed that all birds ringed in year 1 are actually ringed at the beginning of that year. The calculations for a year include a summer period and the subsequent winter period. Only birds marked when at least one year old are included. The number assumed dead is calculated from the number acutally recovered dead, using a recovery rate of 24% (see Fig. 2). The number estimated to be alive is the sum of the number ringed that year plus the number still alive in the previous year minus the number assumed to have died.

year 1	year 2	*n* ringed	estim. alive	recovered, *n*			estimated mortality, %		
				summer	winter	total	summer	winter	total
1983	1984	211	211	1	4	5	2.0	8.0	10.0
1984	1985	108	298	0	25	25	0	35.2	35.2
1985	1986	53	246	3	8	11	5.1	13.7	18.8
1986	1987	131	331	3	20	23	3.8	25.4	29.2
1987	1988	46	280	2	0	2	3.0	0	3.0
1988	1989	12	284	4	3	7	5.9	4.4	10.4
1989	1990	14	268	4	1	5	6.3	1.6	7.8
1990	1991	2	249	4	3	7	6.7	5.1	11.8
1991	1992	9	229	2	1	3	3.7	1.8	5.5
1992	1993	8	224	5	3	8	9.4	5.6	15.0
1993	1994	4	195	3	3	6	6.5	6.5	12.9
1994	1995	10	180	2	1	3	4.7	2.3	7.0
1995	1996	3	170	0	17	17	0	4	42.0

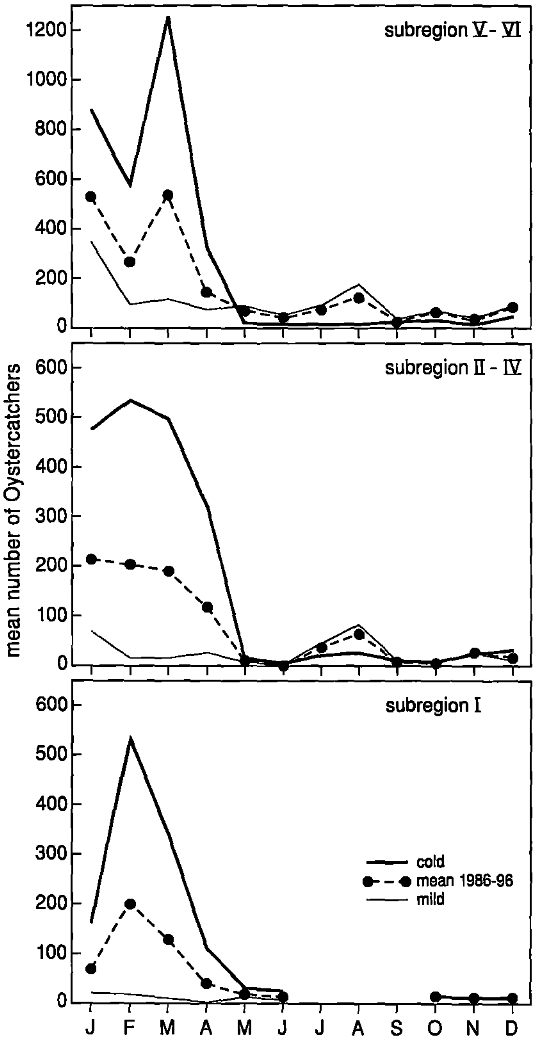

Fig. 6. Seasonal pattern in dead Oystercatchers recorded along the North Sea and Wadden Sea coast, based on monthly beached bird surveys from January 1986-March 1996. Shown are the mean total numbers (after extrapolation) over the entire period (symbols and dotted line), during the moderate or severe winters of 1986, 1987, 1991, and 1996 (thick line) and during the remaining mild winters (narrow line).

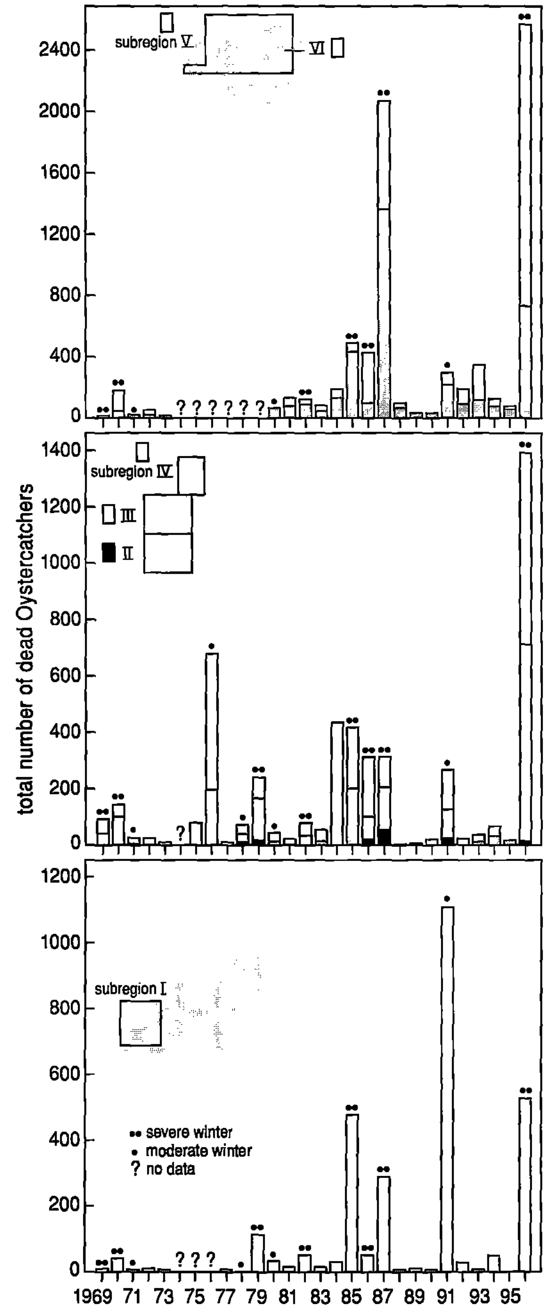

Fig. 7. Number of Oystercatchers found dead per subregion (I, II-IV combined and V-VI combined) during national surveys late February 1969-1996 (Camphuysen 1992 and NZG/NSO unpubl. data). Shown are extrapolated numbers, using observed densities in each subregion. Missing values are indicated by '?' symbols. Severe (**) and moderate winters (*) are indicated on top of each bar.

Table 6. Annual mortality estimates for the population studies on Schiermonnikoog. See Table 5 for conventions.

year 1	year 2	*n* ringed	estim. alive	recovered, *n*			estimated mortality, %		
				summer	winter	total	summer	winter	total
1983	1984	201	201	1	1	2	2.1	2.1	4.2
1984	1985	125	318	3	3	6	4.0	4.0	7.9
1985	1986	70	362	5	3	8	5.8	3.5	9.3
1986	1987	93	422	6	23	29	6.0	22.9	28.9
1987	1988	191	491	2	0	2	1.7	0	1.7
1988	1989	179	662	1	3	4	0.6	1.9	2.5
1989	1990	67	712	4	3	7	2.4	1.8	4.1
1990	1991	68	750	1	7	8	0.6	3.9	4.5
1991	1992	11	728	3	2	5	1.7	1.2	2.9
1992	1993	58	765	4	9	13	2.2	4.9	7.1
1993	1994	18	728	5	3	8	2.9	1.7	4.6
1994	1995	10	705	5	6	11	3.0	3.6	6.6
1995	1996	27	685	5	30	35	3.1	18.4	21.4

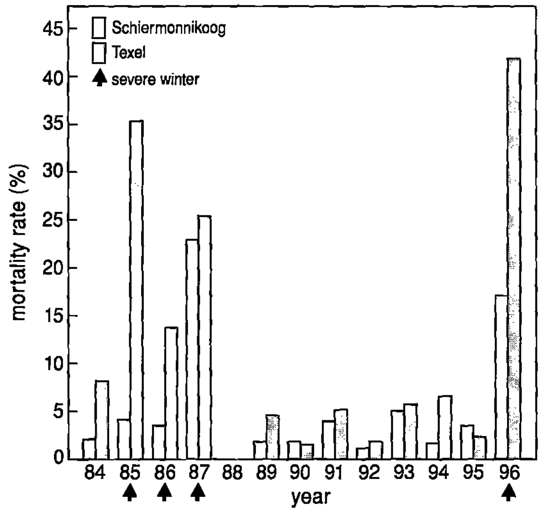

Fig. 8. The estimated winter mortality (September-March) for different years on Schiermonnikoog (entire study area) and Texel (Table 5). Mortality was estimated from ringing recoveries using a reporting rate of 23.8% obtained from observations in the main study area of Schiermonnikoog (see 'Methods' and Fig. 2 for a full explanation). Arrows indicate severe winters.

Oystercatchers in the other subregions were low or close to normal. Upward deviations from the mean annual total of c. 3260 ± 3380 dead Oystercatchers were most pronounced in the cold winters of 1986/1987 and 1995/1996 and these were recorded in all subregions. In these two years, more Oystercatchers were found dead along the North Sea coast (subregions I-V; c. 8200 in 1987 and c. 5500 in 1996) than were estimated to occur in the region from censuses in three mild winters (3000-3400 individuals). This indicates that severe winters must have led to a significant increase in wintering numbers along the coast. In six mild winters (1988-1990, 1992, 1994-1995), estimated totals for January-March ranged from 90 to 400 (mean 246 ± 144 *SD*), or c. 8% of the coastal wintering population.

An examination of the seasonal pattern in dead Oystercatchers showed that peak Oystercatcher numbers along the coast were generally recorded from January to March (Fig. 6). This winter peak was most pronounced in cold winters (e.g. 1986, 1987, 1991, and 1996). In mild winters, comparatively large numbers of dead Oystercatchers were recorded in late summer. Ringing recoveries from the population studies (discussed below) yielded a very similar pattern. Most recov-

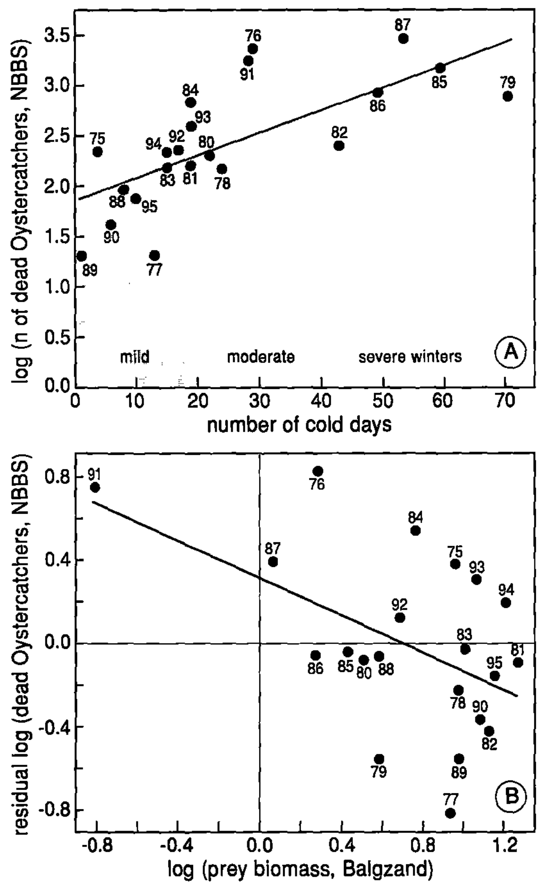

Fig. 9. Relationship between the frequency of cold days (n) and log transformed total numbers of dead Oystercatchers along the coast, based on national beached bird surveys (NBBS), late February 1975-1996 (top) and the relationship between the log transformed total biomass of Cockles and Mussels in the Balgzand area and the residual of dead Oystercatchers in the national beached bird survey, 1975-1994 (bottom).

eries were from severe winters and then rather few birds were recovered in summer (Tables 5 & 6). When winters were mild, comparatively many birds were reported dead during the summer season, although there was no indication that actually more birds died in summers following mild winters.

The national beached bird surveys (NBBS) during 1986-1996 reflected mortality patterns established from the monthly BBS winter surveys fairly well and the correlation between the two data sets was highly significant (Table 7). Numbers of dead Oystercatchers on the Dutch coast recorded in the NBBS fluctuated between c. 20 (1973, 1989) and over 4300 individuals (1996) (Fig. 7). Table 8 shows that peaks in mortality often coincided with severe winters. For 1984-1996 we can also compare this pattern to the mortality estimates from the population studies in the Wadden Sea. Correlations between the NBBS data and the population study data, as well as between population studies themselves were generally high and statistically significant, irrespective whether total mortality was considered or winter mortality only (Table 7). A closer examination of the pat-

Table 7. Comparison of different data sets on Oystercatcher mortality, i.e. the national beached birds survey in February (NBBS), the annual total for the monthly beached bird survey (BBS), the winter mortality in the population study on Schiermonnikoog (Schier) and the winter mortality in the population study on Texel (Texel). The top triangle of the matrix refers to correlation coefficients of correlations on log-transformed data (because mortalities could be zero, the original value plus 1 was logged). The bottom triangle to non-parametric Spearman rank correlations. In brackets the numer of years; stars indicate 1-tailed levels of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	NBBS	BBS	Schier	Texel
NBBS		0.92(10)***	0.82(13)***	0.82(13)***
BBS	0.90(10)***		0.82(10)**	0.75(10)**
Schier	0.79(13)**	0.65(10)*		0.80(13)***
Texel	0.82(13)***	0.66(10)*	0.73(13)**	

Table 8. Regional densities (n km^{-1}, I-VI; see Fig. 1) of dead Oystercatchers, rounded national total numbers (n) and overall densities of dead Oystercatchers in national beached bird surveys between 1969 and 1996 in relation to the severity of each winter (number of frost days and qualification). No survey was conducted in 1974, whereas surveys in 1975-1980 did not cover all subregions. Densities in parantheses represent values based on poorly covered subregions (< 5% of total coastline surveyed). Total numbers of Oystercatchers include extrapolated figures if subregions were not covered completely, to allow comparisons between years. Mortality peaks (i.e. density > 1.0 km^{-1}) are indicated with '→'.

	regional densities (n km^{-1})							dead Oystercatchers		winter conditions	
year	I	II	III	IV	V	VI	total	n	n km^{-1}	frost days	severity
1969	0.1	0.0	0.6	0.6	0.1	0	420	110	0.16	44	severe
1970	0.3	0.1	1.5	0.5	0.2	0.7	415	350	0.52	59	severe
1971	0.0	0.1	0.1	0.2	0.0	0.1	377	40	0.06	34	moderate
1972	0.1	0	0.1	0.2	0.1	0.2	339	80	0.12	15	mild
1973	0.1	0	0.0	0.1	0.0	0.0	420	20	0.03	13	mild
1974	-	-	-	-	-	-	-	?		11	mild
1975	-	0	0	0.8	(0.2)	-	138	> 110	0.30	4	mild
1976	-	0.2	2.9	5.1	-	-	156	> 670	→ 3.13	29	moderate
1977	0.0	0	0.1	0.0	-	-	243	> 10	0.03	13	mild
1978	0	0.2	0.4	0.4	-	-	221	> 70	0.21	24	moderate
1979	0.9	0.3	2.4	0.8	-	-	136	> 350	→ 1.06	70	severe
1980	0.3	0	0.1	0.3	0.4	-	194	> 130	0.27	22	moderate
1981	0.1	0	0.0	0.2	0.5	0.3	344	150	0.22	19	mild
1982	0.4	0.1	0.5	0.5	0.6	0.1	449	240	0.36	43	severe
1983	0.1	0.0	0.1	0.4	0.2	0.2	445	140	0.21	15	mild
1984	0.3	0	0.0	4.5	0.8	0.3	404	640	0.96	19	mild
1985	4.1	0.1	3.2	2.2	3.0	0.3	370	1370	→ 2.04	59	severe
1986	0.4	0.2	1.4	2.2	0.6	1.8	259	770	→ 1.15	49	severe
1987	2.5	0.7	2.6	1.1	9.2	3.7	416	2660	→ 3.97	53	severe
1988	0.0	0.0	0	0	0.4	0.1	450	90	0.13	8	mild
1989	0.1	0	0.0	0.0	0.0	0.0	308	20	0.03	1	mild
1990	0.0	0.0	0	0.2	0.1	0.0	288	40	0.06	6	mild
1991	9.5	0.4	1.5	1.5	(1.4)	(0.4)	251	1650	→ 2.46	28	moderate
1992	0.2	0	0.0	0.2	(0.6)	(0.5)	165	220	0.33	17	mild
1993	0.0	0.0	0.1	0.3	0.8	1.2	315	370	0.55	19	mild
1994	0.4	0.1	0.4	0.3	0.5	0.3	292	230	0.34	15	mild
1995	0	0	0.0	0.1	0.4	0.1	219	80	0.12	10	mild
1996	3.2	0.3	11.5	7.2	4.9	9.6	277	4320	→ 6.45	64	severe

tern reveals that for Schiermonnikoog the two mortality estimates yield very similar results with very high peaks for the severe winters of 1987 and 1996 (Fig. 8). High mortality in these winters is also evident for Texel. Furthermore, both data sets offer indications that mortality was high in 1985 and 1986, the other two severe winters in this period. The 1985 mortality was rather extreme on Texel, but this may be related to the fact that in the preceding two years birds were mainly caught on a roost occupied by poor quality birds (Swennen 1984). After 1985 the emphasis of the study on Texel shifted to sites where survival prospects were probably higher.

Despite some discrepancies, the overall correspondence between the NBBS data and the other data sets is clearly sufficient to exploit more fully the main advantage of the NBBS data: the much longer time span that is covered. The logged numbers of dead Oystercatchers recorded along the coast in national beached bird surveys since 1975 were positively correlated with the frequency of cold days in each winter ($r = 0.71$, $t = 4.37$, $p < 0.01$, $n = 21$; Fig. 9). However, although large numbers of Oystercatchers were found in the severe winters of 1979, 1985, 1986, 1987, and 1996, rather low numbers were recorded in 1982. On the other hand, high figures were reached in the moderate winters of 1976 and 1991. Although low numbers of dead Oystercatchers were found in all mild winters, the results suggest that the frequency of occurrence of low temperatures alone is an inaccurate predictor of the magnitude of mortality among Oystercatchers along the coast. Therefore, the influence of prey availability needs also to be investigated.

Fluctuations in prey stock

Fluctuations of the main prey of Oystercatchers in the Balgzand area (western Wadden Sea) are shown in Table 9 and Fig. 10. Rather low levels in principal prey stock (particularly Cockles and Mussels) were observed in 1976, 1979, 1980, 1986, 1987, and 1988. Exceptionally low levels of Cockles and Mussels were reported in 1991, as a result of stock depletion due to overfishing and recruitment failure (Beukema 1993). We assume that prey availability will be reduced in severe winter conditions, so that a low stock, a severe winter, or a combination would result in elevated mortality rates of wintering Oystercatchers.

Oystercatcher mortality in relation to cold weather and fluctuations in prey biomass

Generally, low biomass levels coincided with high mortality rates among coastal Oystercatchers and often with cold seasons. A negative correlation was found between the residual of log transformed numbers of dead Oystercatchers found in the NBBS and the biomass of Cockles and Mussels in the Balgzand area (Fig. 9). Multiple regression analysis of the number of dead Oystercatchers (log transformed) on the number of cold days and on the biomass of benthic prey (log transformed) revealed an explained variance of 66% ($n = 21$). Both the number of cold days ($t_{18} = 3.37$, $p = 0.003$) and prey biomass ($t_{18} = 2.88$, $p = 0.010$) had a significant effect. The results explain the relatively high mortality among Oystercatchers in the moderate winters of 1976 and 1991

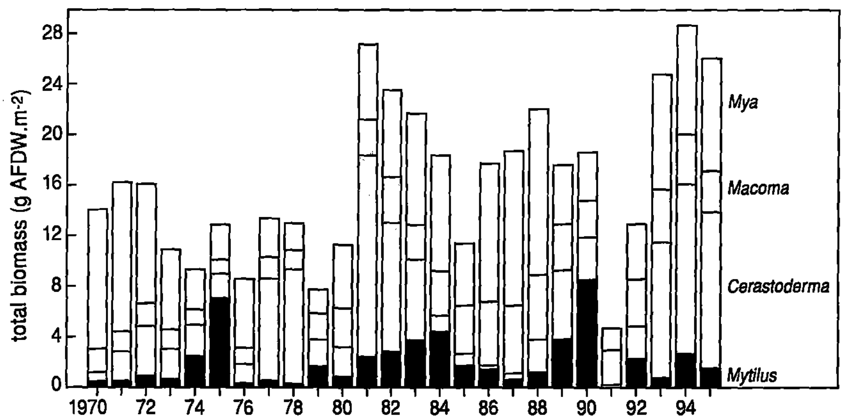

Fig. 10. Total biomass (g m^{-2} ash-free dry weight) of *Mytilus edulis, Cerastoderma edule, Macoma balthica,* and *Mya arenaria* in late winter in the Balgzand area, 1970-1995. Shown is the annual mean in February-March over 15 sampling stations (data courtesy J. Beukema and W. de Bruin, NIOZ).

Table 9. Fluctuations in mean biomass (based on measurements g m^{-2} ash-free dry weight, AFDW) of *Arenicola marina, Carcinus maenas, Cerastoderma edule, Macoma balthica, Mya arenaria, Mytilus edulis, Nereis diversicolor*, and *Scrobicularia plana* over 15 sampling stations in the Balgzand area (western Wadden Sea), late winter (February-March) 1970-1995 (courtesy J. Beukema, W. de Bruin and R. Dekker, NIOZ).Very low (○○; less than half the mean), low (○; less than mean - *SE*), mean (~), high (●; more than mean + *SE*) and very high (●●; more than twice the mean) values are marked. Winters in which excessive mortality among coastal Oystercatchers was recorded during national beached bird surveys are indicated with → (see table 5).

	Arenic.	*Carcinus*	*Cerast.*	*Macoma*	*Mya*	*Mytilus*	*Nereis*	*Scrobic.*
1970	~	○	○○	○	●	○○	○○	○
1971	~	○○	○	○	●	○○	○○	○
1972	●	○○	~	○	●	○○	○○	○○
1973	○	○○	○	○	~	○○	○○	~
1974	○	●●	○	○○	○○	●	○○	○
1975	○	●	○○	○○	○○	●●	○○	○
1976→	○	●	○○	○○	○	○○	○○	○○
1977	○	~	●	○	○○	○○	○○	○○
1978	○	○○	●	○	○○	○○	○○	○○
1979→	○	○	○○	○	○○	○	○	○
1980	○	○	○○	~	○	○○	~	○
1981	~	○	●●	~	~	~	○	○
1982	●	●	●●	●	~	●	○	~
1983	~	○	●	~	●	●	○	~
1984	●	~	○○	●	●	●●	●	●
1985→	●	○	○○	●	○	~	●	●
1986→	●	○○	○○	●	●	○	●	●
1987→	~	○○	○○	●	●	○○	●	○
1988	●	○	○	●	●●	○	●●	○
1989	●	~	~	●	○	●	~	○
1990	●	●●	○	~	○	●●	●	○○
1991→	○	○	○○	~	○○	○○	●	○
1992	●	●●	○	●	○	~	●●	●
1993	●	~	●●	●	●	○○	~	●●
1994	●	○○	●●	●	●	●	●	●●
1995	●	●●	●●	●	●	○	●	●●
mean	4.8	0.1	4.6	2.9	6.5	2.1	1.5	0.3
SE	0.26	0.02	0.87	0.24	0.69	0.39	0.22	0.04
min	1.0	0.0	0.2	1.1	0.8	0.0	0.4	0.1
max	7.2	0.4	16.0	5.4	13.1	8.4	5.2	0.9

(very low food stock), and the low mortality rates in the severe winter of 1982 (large food stock). Furthermore, the excessive mortality observed in 1987 is now explained by a combination of low food stock and severe weather. In the moderate winter of 1991, with extremely low food supply in the Wadden Sea area, most dead Oystercatchers were reported from the Delta area. These results are in contrast to high mortality in severe winters, when elevated numbers of dead birds were mainly reported along the mainland coast and in the Wadden Sea area (Fig. 7).

DISCUSSION

Counts of dead Oystercatchers during BBS not only reflect fluctuations in mortality rates, but also in the use of coastal sites by these birds. In summer, most Oystercatchers stay inland or on Wadden Sea mudflats, and only small numbers occur along the beaches and dikes. In winter, the coastal zone gains in importance but the majority of the wintering Oystercatcher population is still found feeding on intertidal mudflats in the Wadden Sea or the Delta area (SOVON 1988, Meltofte *et al.* 1994). Poor feeding conditions in severe winters due to ice cover and high energy demands or when food stocks are low may force a substantial proportion of these wintering birds to disperse and seek refuge along the coast or to move further south. As a result, the increased numbers of corpses recorded along the coast during beached bird surveys reflect increased numbers of birds using the coast and/or elevated mortality rates of Oystercatchers.

One of the main shortcomings of the use of beached bird surveys is that the true 'mortality rates' (i.e. the number of dead Oystercatchers as fraction of the population) and, hence, that the total mortality cannot be estimated. However, mortality rates estimated from ringing recoveries and re-sightings of marked birds revealed similar patterns. A comparable analysis of mortality of marked Oystercatchers along the Frisian coast also indicated high mortality during severe winters (Zwarts *et al.* 1996c). Apparently, patterns in mortality due to variations in winter severity are rather well described using BBS data. However, the high mortality observed among Oystercatchers in the Delta area in winter 1991 was not reflected in these ringing schemes in the Wadden Sea. The discrepancy could be explained if the Oystercathers which left the Wadden Sea and died in the Delta in 1991 were not local breeding birds but were birds that came from elsewhere to winter in The Netherlands. Such non-local birds tend to have a low social dominance (Ens unpubl.) and will suffer much when competing for food (Ens & Cayford 1996). Another discrepancy is the exceptional mortality among Oystercatchers in BBS results in the eastern Wadden Sea in the mild winter of 1992/1993 (Fig. 5), which was not clearly reflected in ringing data from the area. Hulscher *et al.* (1993) found that Oystercatchers in this area suffered from strong winds resulting in raised waterlevels, during which the available feeding time was shorter than required for the birds to meet the daily food requirements, and so unusually large numbers of Oystercatchers fed on inland sites. Apparently, again mainly non-local birds were affected during this incident. While BBS results deal with mortality patterns in the entire wintering population in The Netherlands (c. 300 000 individuals), the ringing schemes above reflect trends in a rather small, local breeding populations (c. 10 000).

The winters of 1969, 1970, 1979, 1982, 1985-1987, and 1996 stand out as particularly cold seasons. High mortality rates among wintering Oystercatchers along the coast were recorded in the four most recent cold winters and in the moderate winters of 1976 and 1991. In contrast, the severe winters of 1979 and 1982 did produce large numbers of dead Oystercatchers, but not quite so many as were found in 1987 and 1996. The analysis of monthly beached bird surveys showed that nearly 12 000 Oystercatchers were found dead along the coast in 1986/1987 and at least 10 000 in 1995/1996. These figures are still rather low compared to an expected mortality of 75 000 birds (25% of the wintering population; Hulscher 1989). In both years, very large numbers of dead Oystercatchers were found on high tide roosts scattered around the Wadden Sea and in the Delta area and were not included in BBS results.

Stock assessments of benthic prey in the Western Wadden Sea during 1975-1994 suggest that the availability of prey was relatively low in 1976, 1979, 1980, 1985-1987 and in 1991 (Table 9). Several of these years were labelled earlier as 'cold' winters, but the overlap is not complete. The results presented in this paper strongly suggest that either low prey stock (1976, 1991), or prolonged periods of low temperatures (1979, 1985-1987, 1996), or combinations of the two may trigger the dispersal of Oystercatchers away from the normal wintering areas. Cold-rushes, or rather mass departures in response to poor feeding conditions, have been observed in nearly all the winters listed here, leading to relatively low wintering numbers in the Wadden Sea (Fig. 3), increases in the Delta area and probably along the coast, and high mortality levels in the beached bird surveys under study. A notable exception was the severe winter of 1982 in which mass departures were recorded along the mainland coast, but when mortality at coastal sites remained low. The exceptionally favourable feeding conditions in 1982 (Table 9) may have saved the birds this winter.

The effects of severe winters and associated periods of low availability of food for Oystercatchers are quite spectacular in terms of the numbers of birds that die from starvation. Swennen & Duiven (1983) demonstrated that, at least in some of these winters, immatures and unfit individuals numerically dominated the casualties found along the coast. Similarly, hardly any of the juveniles born in 1986 and 1995 survived the following severe winter (Kersten & Brenninkmeijer 1995, Hulscher unpubl.). The spectacular mortality found in 1987 and 1996, however, included substantial numbers of adults (Camphuysen unpubl.).

High mortality levels among Oystercatchers in 1991, although clearly lower than in the severe winters of 1987 and 1996 when substantial icing prevented the birds from feeding and when significant numbers died from starvation, were induced by exceptionally low prey stocks. In the course of 1990, virtually all wild mussel beds in the Wadden Sea disappeared from the tidal flats as a result of intensive fishing (Dankers 1993). As a consequence of failing reproduction in 1988, 1989, and 1990, worsened by a continuation of intensive fishery for Cockles through 1990, the abundance of Cockles reached a minimum in winter 1990/1991 (Beukema 1993). The consequences of coinciding low stocks of Cockles and Mussels were quite dramatic for the Eider population wintering in the Dutch Wadden Sea, leading to major shifts in wintering distribution and a threefold higher mortality than usual (Swennen 1991, Van de Kuip 1991, Camphuysen 1996). As can be seen from the results of beached bird surveys presented in this paper, for Oystercatchers the scarcity of their principal prey due to overfishing has also taken its toll. Had this season also been a cold winter, our results suggest that the mortality would have been unprecedented.

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SAMENVATTING

Veruit de grootste aantallen in Nederland overwinterende Scholeksters worden aangetroffen in het Waddengebied (gemiddeld c. 200 000 exemplaren), maar daarnaast komt een groot aantal overwinteraars voor in de Zeeuwse en Zuidhollandse delta (gemiddeld c. 90 000). In zachte winters komt ongeveer 1% van het aantal overwinteraars in Nederland voor langs de Noordzeestranden. In koude winters kunnen binnen overwinterende populaties in W. Europa omvangrijke verschuivingen optreden. Deense en Duitse overwinteraars trekken naar het Nederlandse Waddengebied, terwijl de normaal in het Nederlandse Waddengebied overwinterende Scholeksters naar de Delta trekken, en gedeeltes van deze populaties trekken soms nog verder weg naar het zuiden. In strenge winters neemt het aantal overwinteraars in de Nederlandse Waddenzee af als gevolg van deze verschuivingen, terwijl het Deltagebied aan betekenis wint. Langs de Noordzeestranden komen in koude jaren meer Scholeksters voor dan in minder koude winters. De verschuivingen onder de overwinteraars gaan dikwijls gepaard met indrukwekkende 'vorstvluchten'. Langs de kust worden in koude jaren veel meer dode Scholeksters aangetroffen dan in milde winters.

De sterfte van Scholeksters in een reeks van winters werd bestudeerd aan de hand van tellingen van dode Scholeksters langs de kust (1969-1996) en aan de hand van zichtwaarnemingen en terugmeldingen van Scholeksters geringd op Schiermonnikoog en Texel. Fluctuaties in sterfte werden vervolgens in verband gebracht met het voorkomen van vorstperioden en met het voedselaanbod. Verondersteld werd, dat een koude winter de beschikbaarheid van het voedsel op het wad zou doen teruglopen (ijs op het wad), zodat verhoogde sterfte zou optreden in jaren met (1) weinig voedsel, (2) langdurige vorstperioden, of (3) beiden. Een belangrijke reden voor de analyse was het nagaan van de effecten op Scholekstermortaliteit van de intensieve bevissing van schelpdieren in de Waddenzee die er in 1991 toe leidde dat Kokkels en Mossels vrijwel totaal verdwenen waren in het Waddengebied. Multipele regressie analyse van de aantallen dode Scholeksters langs de kust in de jaren 1975-1996 (de jaren met de meest betrouwbare gegevens), het aantal vorstdagen in elke winter en de biomassa aan prooien in de westelijke Waddenzee leidde tot een verklaarde variantie van 66% ($n = 21$). Zowel het aantal vorstdagen als de voedselvoorraden droegen significant bij aan de gemeten Scholekstersterfte. De resultaten verklaarden de relatief hoge sterfte in 1976 en 1991 (zeer gering voedselaanbod) en de geringe sterfte in 1982 (koude winter met enorm voedselaanbod). De exceptionele sterfte van 1987 was het gevolg van een combinatie van gering voedselaanbod en een koude winter. Er zijn aanwijzingen dat de sterfte vooral plaatsvond onder normaal niet in Nederland overwinterende Scholeksters die vermoedelijk minder goed dan lokale vogels in staat waren om voedselterritoria veilig te stellen. De overbevissing van schelpdieren in 1990-1991 heeft ertoe geleid dat grote aantallen Scholeksters uit de Waddenzee vertrokken, maar deze vogels kwamen in het Deltagebied vervolgens massaal om het leven. De resultaten suggereren dat het voorkomen van langdurige koude omstandigheden in de vrij milde winter van 1990/1991 tot een ongekende mortaliteit onder Scholeksters zou hebben geleid.